

Color Pattern of the Eastern Pacific Spotted Porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae)

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(Plates I-VII; Text-figures 1-3)

Developmental, individual, and between-school variation in coloration is described. New-born are unspotted, and are dark-gray above and white below. Dark-gray ventral spots appear first at side of jaw and in area ahead of flipper, then develop rapidly over entire ventral surface. Ventral spots fuse in adults to yield uniform gray appearance below. Dorsal light-gray spots begin to develop after appearance of ventral spots and vary greatly in size and density in adults. System of markings about head, including eye patch, eye band, gape border, forward extension of cape mark, and flipper band, reach highest degree of contrast with ground coloration in subadults and persists only faintly in adults. Features that show great individual variation include extent of secondary dark-gray brushings on head of newborn and development of dorsal spotting in adults. Features showing variation between schools include structure of flipper band, definition of cape mark, definition of secondary light-gray band below cape mark, and color of tips of jaws. Coloration is similar to *S. attenuata* except for contrast between components of pattern, but different from that of *S. plagiodon*.

INTRODUCTION

PORPOISES of the genus *Stenella* are not only of high scientific interest, but are also important to the multimillion-dollar, California-based tropical tuna fishery. Two porpoises — the spotted *Stenella graffmani* (Lönnberg), and a form called “spinner porpoise” by fishermen, assigned to *S. microps* (Gray) by Handley (Hester, Hunter, and Whitney, 1963) and to *S. longirostris* (Gray) by Nelson (1889) and Hershkovitz (1966) — and yellowfin tuna, *Thunnus albacares* (Bonnaterre) occur together in large school complexes in the eastern central Pacific. Fishermen locate the tuna by spotting the porpoise schools at the surface. The association between fish and the porpoise is very close, and the fish schools can be slowed, consolidated, and otherwise directed by herding the porpoise (Inter-American Tropical Tuna Commission, 1968; McNeely, 1961; Perrin, 1968). Despite their economic importance, little is known of the biology of either of the porpoises. The present report describes color pattern development

and color variation within and between schools of *Stenella graffmani*.

Little has been recorded about the coloration of *S. graffmani* since it was described by Lönnberg (1934) from a salted skin and part of the skull of a large male collected near Acapulco, Guerrero, Mexico. He described the skin as follows: “The colour of the skin, since the salt had been removed, was coal black all over but with small scattered, whitish-gray spots, chiefly on the back, and perhaps more numerous on the back behind the dorsal fin. On the lower parts of the sides these spots were much less numerous and much smaller in size than those of the back.” His figure of the type-specimen was based on a photograph of the dried skin after it had been partially prepared for mounting. The spotting described by Lönnberg is evident in his figure, but a characteristic ground pattern, described below, apparently was obliterated by the salting process.

Hall and Kelson (1959), perhaps following Lönnberg’s description, described *S. graffmani* as “blackish throughout, mottled dorsally with grayish-white.” Walker (1964) published a good lateral photograph of what appears to have been

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a large adult female. The spotting pattern is easily seen, and some elements of the ground pattern are discernible. Ingles' (1965) wash drawing is inaccurate in shape and coloration. A drawing published by Daugherty (1965) depicts the shape of the animal more accurately but represents the color pattern poorly. She described the pattern as "... uniform gray, with scattered small spots of white or light gray. The spotting is variable, sometimes being quite conspicuous, especially in certain body areas, at other times being hardly noticeable. It is undoubtedly more distinct in live animals than in the dead ones which the tuna boats bring in."

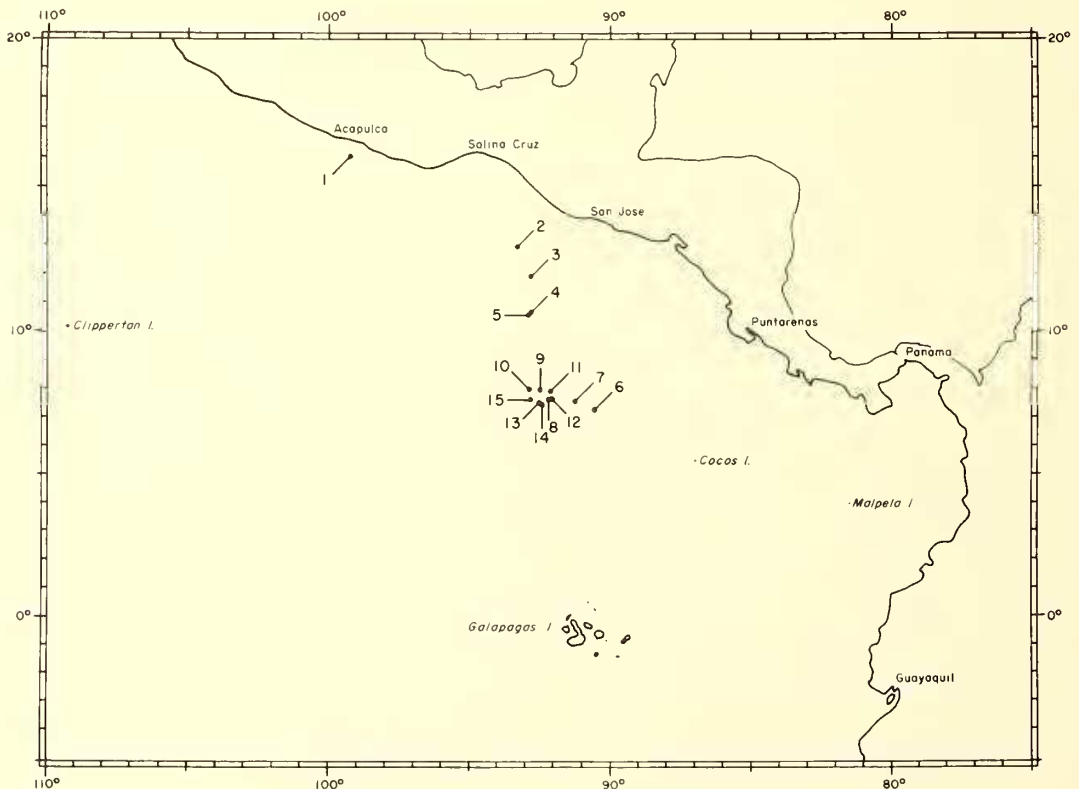
The only previously published observation on the variation of coloration other than in adult specimens of *S. graffmani* is the report by Caldwell and Caldwell (1966) of an unspotted calf taken from the uterus of a spotted mother. As is shown below, this difference is a function of age.

The inadequacy of the record can be laid to the difficulty of obtaining and studying specimens, especially fresh ones, of a tropical pelagic cetacean such as *S. graffmani*. American tuna fishermen have in recent years begun to use very large purse seines in areas where schools of

S. graffmani are closely associated with tuna schools. This circumstance has lately made the species accessible to study.

MATERIALS AND METHODS

This report is based on specimens, notes, and photographs that I collected during a cruise to the eastern central Pacific aboard a commercial tuna seiner, from April 1 to April 29, 1968. Fifteen net sets, numbered 1 to 15 (Text-fig. 1), were made on porpoise from tuna-porpoise associations. Since deck space was required for examination of the animals, the amount of data that I could collect from a particular set depended on the time of day, the amount of fish in the net, and other factors that affected the fishing operation. Extensive observations on large numbers of animals could be made only when the net set was completed at or near the end of the fishing day; it was then possible to keep porpoise on deck until the following morning. Some color observations were made on all 15 of the school samples, and more detailed notes were taken on 129 specimens from four schools. Extensive morphometric and ecological data that were gathered will be reported elsewhere.



TEXT-FIG. 1. Locations of net sets numbers 1-15. *Stenella graffmani* was taken in all sets except no. 14.

The degree of sexual development of 107 animals was estimated by a rapid field examination of the gonads. Males with full-size testes (approximately 30 cm in length) were adjudged mature. The females that were not pregnant or lactating fell into two groups, those in which both ovaries were flat and obviously immature and those in which one or both ovaries were fully developed and contained corpora albicantia or maturing follicles. Since gonads were not examined histologically, the determinations of maturity must be considered estimates.

DEVELOPMENTAL AND INDIVIDUAL VARIATION

When a number of spotted porpoise from a single school are laid on the deck of a ship, the first impression is one of wide variation in coloration. In the schools I examined, however, the animals could be grouped roughly into the following five general categories of color pattern (Pl. I):

a. *Newborn stage.* Dark purplish-gray dorsal surfaces and lateral brushings, with white ventral surfaces and no spots; displayed by the smallest individuals, some of which retained shreds of umbilical cord.

b. *Two-tone stage.* General two-tone pattern with dark-gray surfaces above, lighter-gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots. The individuals in this and the following two groups were progressively intermediate in size between the smallest (newborn) and largest animals.

c. *Speckled stage.* Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others.

d. *Mottled stage.* Ventral spots converging and overlapping in places, but patches of the lighter-gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces.

e. *Fused stage.* Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; displayed by the largest individuals.

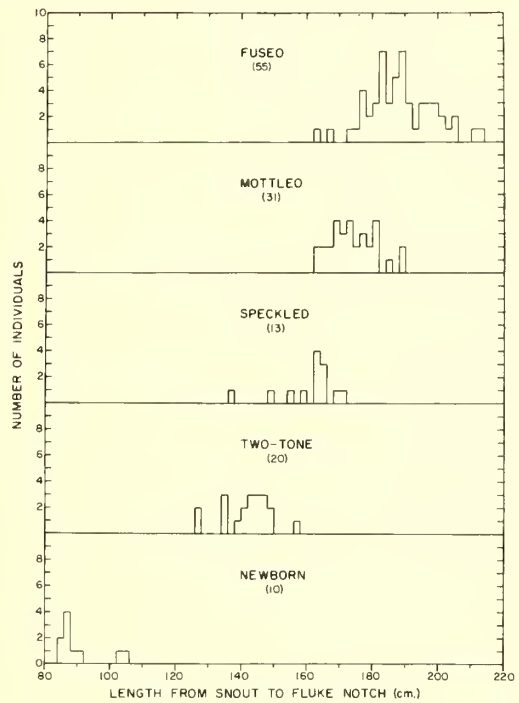
These five categories represent definable increments in a continuous development of coloration. The rather close correlation between these pattern categories and the size of the animals (Text-fig. 2) demonstrates clearly that the primary component of the spotting variation is developmental. An alternative explanation—that size, and therefore spotting development, are

independent of age—is eliminated by data on maturity (Table 1). None of the two-tone or speckled animals were sexually mature; nearly one-third of the mottled animals were mature; and all but one of the fused individuals were mature. This sequence indicates that the onset of sexual maturity occurs during or shortly after the mottled stage.

Color of Newborn Animal

The newborn animal (Pl. II, fig. 2) is dark-gray above and creamy-white below. The boundary of a well-defined mark, referred to below as the cape mark, extends from the apex of the melon, over the eye, to behind the dorsal fin. In the latter area, approximately one-fourth of the distance from the dorsal fin to the flukes, the boundary is less sharply delineated. In lateral view, the cape extends approximately two-thirds of the way down the side of the animal above the anterior insertion of the dorsal fin.

The area from the vertical through the genital region to the flukes is sharply divided along a line that runs forward from the lateral fluke origin into a dark-gray area above and a lighter portion below. The area below the line shades from white above the anus to dark-gray



TEXT-FIG. 2. Relationship between size and development of ventral spotting in 129 specimens of *Stenella graffmani*. Sample size is shown in parentheses.

TABLE 1.
RELATIONSHIP BETWEEN SEXUAL MATURITY AND
DEVELOPMENT OF VENTRAL SPOTTING IN 102
SPECIMENS OF *Stenella graffmani*

Color pattern	Males		Females	
	Number examined	Number mature	Number examined	Number mature
Two-tone	12	0	11	0
Speckled	4	0	5	0
Mottled	14	1	10	6
Fused	13	12	33	33

at the fluke origin. The gray of the upper half of the divided area extends forward and into the cape region, but the margin there is more diffuse. A narrow, diffuse streak of the same shade of gray arises from the lower margin of the dark area at approximately above the posterior insertion of the flipper. It extends posteriorly and slightly into the white area below the cape.

Seen from below, the pure white of the lower surface narrows to a line along the ventral keel at about half the distance between the anus and the fluke notch. The white edging extends to the end of the keel.

Coloration about the eye is distinctive. A dark eye patch is drawn out at its forward margin into a narrow eye band which extends forward along the rostral groove and joins the cape mark near the apex of the melon. This well-defined eye marking is overlaid with a more extensive diffuse marking of lighter-gray. There are brushings of the same gray color on the upper side of the snout and on both sides of the lower jaw. Individual variation is great in the width and definition of the eye band and in the extent of the lighter-gray overlaid markings (Pl. II, fig. 3). Animals with extensive brushing around the eye also have a faint suggestion of a broad, very diffuse band extending from the eye region to the flipper origin.

The flippers and flukes are dark-gray on both surfaces, and the dorsal fin is also uniform dark-gray.

Inferred Development of Coloration

As the porpoise increases in size, the entire region below the cape mark darkens to a light-gray (Pl. II, fig. 4). The secondary brushings about the eye and snout are no longer evident. The eye band becomes part of a well-defined system of connected markings (Text-fig. 3) that includes a dark margin around the most posterior part of the gape and the dark flipper band, which extends from the gape to the anterior insertion of the flipper. This pattern persists throughout further development. Anteriorly the lower margins of the flipper bands extend ventrally, becoming confluent in the gular area about four-fifths of the distance from the tip

of the snout to the end of the gape. There is great interschool variation in the extent and delineation of the flipper band (discussed below). Parallel to the margin of the cape mark is a narrow lighter-gray band, approximately as wide as the eye patch (Pl. III, fig. 5). The band disappears approximately below the dorsal fin tip; definition of the band varies among schools.

The next event in the developmental sequence is the appearance of dark-gray spots on the ventral surfaces. The spots appear first on the side of the lower jaw and in the flipper band near the anterior insertion of the flipper (Pl. III, fig. 6). They seem to appear rapidly during growth over the entire ventral surface, but remain densest on the mandible and in the flipper band (Pl. IV, fig. 7). The spots become larger and begin to overlap (Pl. V, figs. 8 and 9), and the flipper bands become less evident (Pl. VI, figs. 10 and 11). At this stage, the animal has a mottled appearance below. The spotting may extend to both surfaces of the flippers. Individual variation in regularity of size and spacing of the spots results in variable appearance of the ventral aspect during the mottled stage. As growth proceeds, the spots coalesce least rapidly in the gular and genital regions. When fusion is complete, the spots are no longer clearly evident and the animal appears uniform gray below (Pl. VI, figs. 10 and 11), although the spots may still be detected upon close inspection. The pattern about the head, including the eye band and flipper band, is still apparent, but faint.

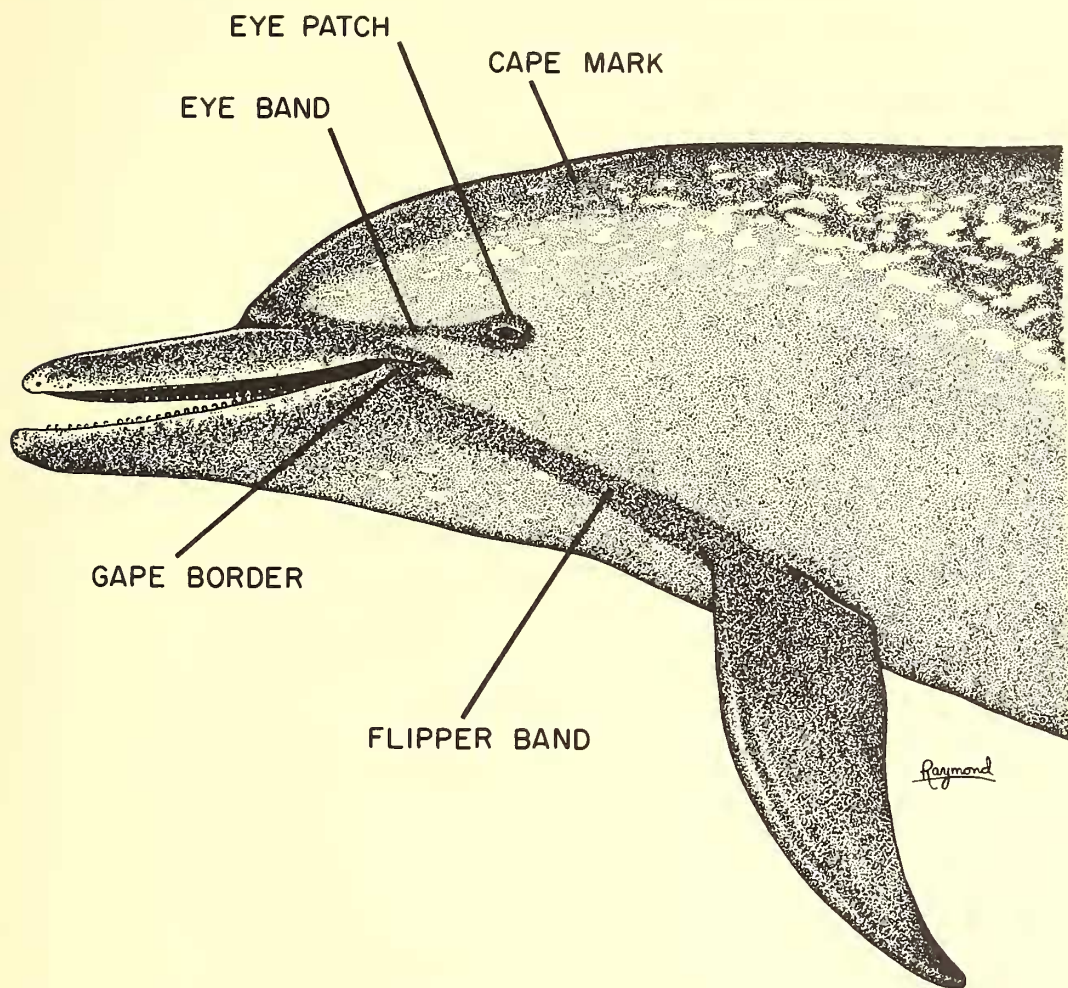
After the ventral dark spots have appeared, very light-gray spots become evident on the dark-gray dorsal surfaces (Pl. V, fig. 8). Their size and number rapidly increase, and they become densest and may overlap at the margin of the cape mark above the eye and in the area immediately posterior to the cape mark (Pl. VI, figs. 10 and 11, and Pl. VII, fig. 12). The density of light spots in these areas and over the rest of the upper surfaces, once the fused stage has been reached, varies within a school (Pl. VII, fig. 13) and bears no apparent relationship to the size of the animal. In some individuals, the light spotting extends to the area below the cape mark.

BETWEEN-SCHOOL VARIATION

In addition to the developmental and individual variation within schools, I observed between-school variation in several features:

1. The structure of the flipper band varied between schools from a simple band (Pl. II, fig. 4) to a wider, more complex structure (Pl. III, fig. 6).

2. The narrow light-gray band contiguous to the cape mark was very strongly defined in the subadults of some schools (Pl. III, fig. 5). The



TEXT-FIG. 3. Pattern on head of adult *Stenella graffmani*, with explanation of terms used in text. Sketched from female, 195 cm, from set no. 7.

presence of this band was correlated with a poorly defined upper margin of the flipper band.

3. The contrast between the cape mark and the lighter lower surfaces varied. The larger individuals taken in set number 5 appeared at first sight to be uniform dark-gray with light dorsal spots. Closer inspection, however, revealed a faint cape mark.

4. In some schools, the larger adults had white-tipped jaws (Pl. VII, fig. 14), correlated with a faint light-gray flecking of the dark-gray ventral surface, especially in the gular region.

On the basis of color notes and photographs, I scored each of five schools for each of these four features (Table 2).

Fraser (1966) posed a stimulating question about schools of tropical *Stenella* species. He asked, "Are the dolphins fortuitously congre-

gated for some purpose such as feeding, breeding, or deriving benefit from especially favorable environmental conditions? Or is each school formed by the natural increase of an isolated family unit?" The between-school differences in coloration detected in *S. graffmani* suggest that schools of this species may constitute genetic entities. Between-school variation in skeletal and external morphometric characters has yet to be examined for any of the spotted porpoises.

COMPARISON WITH OTHER FORMS

The developmental sequence in color pattern parallels that described for *Stenella plagiodon* (Cope)² by Caldwell and Caldwell (1966) except that in *S. plagiodon* the ventral dark spots do not become fused. The adults figured by the

² Placed in the synonymy of *S. pernettyi* (Blaineville) by Hershkovitz (1966).

TABLE 2. BETWEEN-SCHOOL VARIATIONS IN COLOR PATTERN OF SPECIMENS OF *Stenella graffmani* FROM SIX SCHOOLS

The symbol — indicates feature absent or so poorly defined as to appear absent; + indicates feature present and sufficiently well-defined to be readily observable; ++ indicates feature was strikingly well-defined.

Feature	School (set number) and (in parentheses) number of animals examined					
	4 (33)	5 (31)	8 (92)	9 (183)	11 (34)	12 (48)
1. Complex flipper band	—	—	+	+	+	+
2. Secondary light band below cape	+	—	+	+	—	+
3. Contrast between cape and ground	++	—	+	+	+	+
4. White jaw tips	—	—	+	+	++	—

Caldwells and others (True, 1885; McBride, 1940; Moore, 1953) are all spotted or mottled below. Other differences in pattern are evident from the photographs: In *S. plagiodon* the ventral ground is white rather than light-gray; the lateral and dorsal light spotting is developed to a higher degree; the cape mark is apparently present in the unspotted juvenile but is not evident in the photographs of older, spotted animals; and a light line runs from the eye to the posterior insertion of the flipper in unspotted young specimens (absent in *S. graffmani*).

The coloration of the other common spotted porpoises, *S. attenuata* (Gray)³ in the south Atlantic and central and western Pacific and *S. frontalis* (Cuvier) in the Atlantic, is less well known than that of *S. plagiodon*. Photographs of *S. attenuata* from Japan (Nishiwaki, Nakajima, and Kamiya, 1965) show a cape mark and eye and flipper bands like those of some individuals of *S. graffmani*. In reference to spotting, Nishiwaki *et al.* stated “. . . the dorsal half of the body is blueish purple black with numerous gray and white spots, and the ventral half of the body is gray with numerous tiny white spots. There are no spots on the head, the dorsal fin, the flippers, and the tail flukes.” The jaw tips are white. The contrast between the cape mark and the lighter area below appears to be much stronger than in *S. graffmani*. In the specimens of *S. graffmani* that I examined, white jaw tips and white-flecked ventral surfaces were present in some schools, and the degree of light spotting in the dorsal region varied within schools; consequently, the only consistent difference in coloration between the specimens of *S. attenuata* which Nishiwaki *et al.* figured and those of *S. graffmani* described in the present paper is in the degree of contrast between the cape mark and the area below.

Dawbin (1966) published a photograph of six spotted porpoises (heads only) taken by natives on the island of Malaita in the Solomons. He assigned these animals to “the *S. attenuata-frontalis* group.” The portion of the color pattern that can be seen corresponds to the pattern in *S. graffmani* in every respect.

A specimen of *S. frontalis* from the coast of French Equatorial Africa that Fraser (1950) described in great detail did not differ in color pattern from *S. graffmani*. The jaw tips were white, and the ventral surface was “. . . dark gray with abundant darker spots and fewer scattered white spots.” Fraser cited the fact that Lönnberg's (1934) description of the type of *S. graffmani* did not mention a white snout tip and chin and concluded, “It is only in the flecking on the body that this species can, by color, be connected with the ‘Atlantide’ specimen — *S. frontalis*.” White snout tips, as noted above, occur in some individuals of *S. graffmani*. This feature has now been noted in all the spotted porpoises (Nishiwaki, 1965; Dawbin, 1966; Caldwell and Caldwell, 1966).

Of three spotted porpoises from West Africa that Cadenat (1959) described, one that he tentatively referred to as *S. frontalis* corresponds to *S. graffmani* in coloration. The remaining two more closely resemble the specimens of *S. plagiodon* depicted by Caldwell (1966), and he indeed tentatively referred one of them to that species.

The closely similar or identical color patterns of the nominal species of spotted porpoises point out the need for intensive and standardized observations on large series of these animals. From my observations on *S. graffmani* and from previously published descriptions and figures of color patterns in *S. frontalis* and *S. attenuata*, I see no basis at present for separation of these three forms by coloration. This is not to say that they may not prove to be separable on the basis of other characters.

³Placed in the synonymy of *S. dubia* (Cuvier) by Hershkovitz (1966).

The conclusions reached here are tentative, because they are based on data for a relatively small number of schools from a restricted portion of the geographical range of the species. Definition of the total range of variation and more accurate delineation of the developmental, individual, and between-school components of variation must await the availability of larger series, from throughout the range.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. Development of color pattern in *Stenella graffmani*, showing observable increments described in text: a. newborn, b. two-tone, c. speckled, d. mottled, e. fused. Painted by George M. Mattson from photographs and field notes.

PLATE II

- FIG. 2. Newborn *Stenella graffmani*, female, total length (tip of snout to fluke notch) 87 cm. From set no. 5.
- FIG. 3. Lateral views of heads of four newborn female specimens of *Stenella graffmani* from set no. 5. Lengths from left to right: 85 cm, 85 cm, 87 cm (same animal shown in Fig. 2), 86 cm. Note variation in markings about the eye. In the first three individuals the basic dark eye band is overlaid with a more diffuse and more extensive marking of lighter gray.
- FIG. 4. Subadult *Stenella graffmani* at two-tone stage. Female, 141 cm, from set no. 5. The scattered white flecks are adhering fish scales.

PLATE III

- FIG. 5. *Stenella graffmani* at two-tone stage, showing light band below the cape mark. From set no. 8. Sex and length data for this specimen and for others of those figured below were not gathered. The reason for these gaps in the data is explained in the text.
- FIG. 6. *Stenella graffmani*, showing early stage of ventral spot development. From set no. 11.

PLATE IV

FIG. 7. Lateral views of head, middle, and tail regions of *Stenella graffmani* at the speckled stage. Female from set no. 11. The white flecks are adhering fish scales.

PLATE V

- FIG. 8. *Stenella graffmani* at mottled stage. Female, 184 cm, from set no. 12.
- FIG. 9. Ventral views of *Stenella graffmani* at early speckled (lower) and mottled stages. Female (lower), 163 cm; and male, 165 cm, from set no. 10.

PLATE VI

- FIG. 10. Adult *Stenella graffmani* at fused stage with light dorsal and lateral spotting. Male, 187 cm, from set no. 12.
- FIG. 11. Ventral views of three adult specimens of *Stenella graffmani* at fused stage, from set no. 9. From bottom: male, 200 cm; female, 183 cm; female, 176 cm.

PLATE VII

- FIG. 12. *Stenella graffmani* with heavy dorsal and lateral spotting. From set no. 10.
- FIG. 13. Sample from one school of *Stenella graffmani* on deck of tuna seiner. Note variation in dorsal and lateral spotting.
- FIG. 14. Large adult *Stenella graffmani*, showing white jaw tips and lips. From set no. 11.